Prolonged interglacial warmth during the Last Glacial

in northern Europe

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Few fossil-based environmental and climate records in northern Europe are dated to Marine Isotope

Stage (MIS) 5a around ca. 80 kyr BP. We here present multiple environmental and climate proxies

obtained from a lake sequence of MIS 5a age in the Sokli basin (N Finland). Pollen/spores, plant

macrofossils, NPP's (e.g. green-algae), bryozoa, diatoms and chironomids allowed an exceptionally

detailed reconstruction of aquatic and telmatic ecosystem successions related to the development

of the Sokli Ice Lake and subsequent infilling of a relatively small and shallow lake confined to the

Sokli basin. A regional vegetation development typical for the early half of an interglacial is recorded

by the pollen, stomata and plant macrofossil data. Reconstructions of July temperatures based on

pollen assemblages suffer from a large contribution of local pollen from the lake's littoral zone.

Summer temperatures reaching present-day values, inferred for the upper part of the lake

sequence, however, agree with the establishment of pine-dominated boreal forest indicated by the

plant fossil data. Habitat preferences also influence the climate record based on chironomids.

Nevertheless, the climate-optima of the predominant intermediate- to warm-water chironomid taxa

suggest July temperatures exceeding present-day values by up to several degrees, in line with

climate-inferences from a variety of aquatic and wetland plant indicator species. The disequilibrium

between regional vegetation development and warm, insolation-forced summers is also reported for

early-Holocene records from N Fennoscandia. The MIS 5a lake sequence is the last remaining fossil-

bearing deposit in the Late Quaternary basin infill at Sokli to be studied using multi-proxy evidence. A unique detailed climate record for MIS 5 is now available for formerly glaciated N Europe. Our studies indicate that interglacial conditions persisted into MIS 5a, in agreement with data for large parts of the European mainland, shortening the Last Glacial by some 50 kyr to MIS 4-2.

Keywords: MIS 5a interglacial, Last Interglacial Complex, Last Glacial, multi-proxy comparisons, quantitative climate reconstructions, Sokli, high-latitude Europe

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Long proxy climate records, a wide geographical spread of proxy climate data, and quantification of climate parameters are essential for the reconstruction of past climate variability, understanding of forcing mechanisms, and validation of climate model simulations. Long continuous records that predate the present interglacial period (Holocene, i.e. the last ca. 11 kyr) are particularly scarce from high N latitudes due to glacial erosion. In Fennoscandia (N Europe), Late Quaternary (last 130 kyr) environmental and climate conditions have been classically reconstructed through correlation of generally poorly-dated bio/litho-stratigraphic fragments with the NW European mainland climate-stratigraphy and the deep-sea oxygen-isotope stratigraphy (e.g. Lundqvist, 1992; Donner, 1995). As clearly outlined in Donner (1996), the correlations on land were fraught with uncertainties, caused by e.g. the long distance of correlation and truncations of geological beds resulting in incomplete interstadial or interglacial sequences. The marine oxygen-isotope stratigraphy was used as a proxy for global ice volume changes (e.g. Kleman et al., 1997), even though this record carries a composite signal of e.g. ice volume and ocean water temperature (Lisiecki and Raymo, 2005). Furthermore, climate reconstructions were made mostly using pollen data and quantifications of climate parameters were rare.

We here present an environmental and climate record obtained from a lake deposit of Marine Isotope Stage (MIS) 5a age, centred around 82 kyr BP (Lisiecki and Raymo, 2005), found in the Sokli basin in the N boreal forest of NE Finland. The MIS 5a lake sequence forms part of a unique long sedimentary sequence that spans the last 130 kyr (Helmens *et al.*, 2000, 2007) and it is the last remaining fossil-bearing deposit at Sokli to be studied in detail. We use sediment characteristics (lithology, loss-on-ignition (LOI)), pollen and spores, non-pollen palynomorphs (NPP's), macrofossils of plants and zoological taxa, diatoms and chironomids (aquatic insects) to reconstruct in detail local successions in aquatic and telmatic ecosystems, the lake development, and developments in regional vegetation. Mean July air temperatures are quantified by means of plant indicator species identified in the pollen and macrofossil analyses, and by applying the transfer function approach to

pollen and chironomid assemblages. The climate inferences are validated against the local lake development.

We use the data obtained on the MIS 5a lake deposit from Sokli to further explore the interglacial character of MIS 5 as earlier discussed in Helmens (2014). The latter paper compares long terrestrial records from central and N Europe with marine data. It proposes a subdivision of the last climate cycle into an early, overall mild interglacial half (MIS 5) and a late, overall cold glacial half (MIS 4-2), each with duration of ca. 60 kyr. This subdivision deviates from the NW European mainland climate-stratigraphy where the Last Glacial (Weichselian) lasts ca. 100 kyr, starting at the base of MIS 5d at ca. 115 kyr. It also sharply contrasts with earlier reconstructions in Fennoscandia which suggested cold tundra conditions at Sokli, with sub-arctic birch woodland in areas presently covered by mixed boreal forest south of Sokli, during MIS 5c and MIS 5a (e.g. Donner, 1995). The paper by Helmens (2014) used low-resolution pollen data from fragmented core sections to infer past environmental and climate conditions for MIS 5e and 5a at Sokli. The MIS 5e lake deposit has since been studied in detail, and the lake deposit of MIS 5a age is studied here, both using multiple proxies on new boreholes from the Sokli basin.

Present environmental setting and stratigraphy

Study site

The Sokli site is situated in the N boreal forest of NE Finland (lat. 67°48' N, long. 29°18' E, elevation ca. 220 m a.s.l.), on the main water divide that separates drainage into the Barents and White Seas to the east and the Baltic Sea to the southwest. The Sokli wetland (Sokliaapa; Fig. 1) is drained by the Sokli rivulet (Soklioja) that flows to the SW into the Yli-Nuortti river. Bedrock in the region is Precambrian Shield with the exception of the immediate surroundings of the study site that is underlain by Paleozoic carbonate-rich rocks of the Sokli Carbonatite Massif. Dispersed residual

phosphorous deposits occur at the surface of the carbonatite, particularly in the W part of the massif on the slopes above Lake Loitsana (Talvitie *et al.*, 1981).

Present climate at Sokli is cool boreal with mean July and February temperatures of 13 °C and -14 °C, respectively; mean annual precipitation amounts to 500-550 mm (Drebs *et al.*, 2002). Lakes in the area are ice-covered between October and end of May. Mires of the aapa-type (i.e. a patterned fen) with *Sphagnum* spp., *Rubus chamaemorus*, Ericales, *Betula nana*, *Salix* spp*.* and *Carex* spp*.* are extensively present in the region. Birch (*Betula pubescens* and *B. pendula*), pine (*Pinus sylvestris)* and spruce (*Picea abies)* are the dominant tree species in the regional forest. Spruce reaches its northern limit some 100 km north of Sokli (Fig. 4). Farther north, pine forest predominates, succeeded northwards and upwards by birch-pine forest and then sub-arctic birch forest. The forest limit, which is situated some 300 km north of Sokli, is formed by the polycormic mountain birch *B. pubescens* subsp. *czerepanovii*, syn. *tortuosa*. The vegetation of the tundra region beyond the forest limit is low-arctic dwarf-shrub tundra dominated by *B. nana* and Ericales.

Sediment preservation

The Sokli Carbonatite Massif consists of carbonate-rich rocks of magmatic derivations/descent (carbonatite) and a fenite halo. The latter developed by metasomatism of the crystalline rocks that surround the magma intrusions (Vartiainen, 1980). The deeply weathered carbonatite manifests itself in the landscape as a circular depression, ca. 5 km in diameter, bordered by a hilly ring of fenites (Fig. 1). Drillings carried out in connection with carbonatite prospecting revealed a string of hollows, with sedimentary infillings up to 10-30 m thick, that follows a NE-SW trending fracture zone (Talvitie *et al.*, 1981). A 30 m-thick sedimentary sequence that includes a series of thick organic-bearing units of Late Quaternary age occurs in the center of the massif where two fracture zones cross (Ilvonen, 1973a, 1973b; Johansson and Räsänen, 1994; Helmens *et al.*, 2000, 2007a). The latter depression is referred as the Sokli basin (Helmens *et al.*, 2000).

Sokli is located in the E part of a zone, which stretches over central Finnish Lapland, with a concentration of findings of pre-LGM sediments (Hirvas, 1991). This sediment preservation is ascribed to low ice-flow velocities and/or frozen-bed conditions under the central part of the Fennoscandian Ice Sheet (e.g. Kleman *et al.*, 1997). However, a closer look at the till-covered organic beds shows that these beds are generally only a few decimeters thick and often occur in a secondary position, i.e. the sediments are not found *in-situ* but have been truncated and transported by the ice sheet (Hirvas, 1991). This means that, although limited erosion in the ice-divide zone might have contributed to its preservation, the unique preservation in the Sokli basin of multiple, thick fossil-bearing deposits is most probably due to the non-typical bedrock conditions at Sokli. It is the combination of a steep hollow in the relatively soft carbonatite rocks combined with the presence of surrounding hills formed in hard fenite rocks that have provided shelter against glacial erosion. Another site with preservation of a long, 22 m-thick sediment sequence is Rautuvaara in W Finnish Lapland. Here, a series of individual till beds, interbedded with sorted glacio-lacustrine sediment, but not including any organic-rich unit, can be followed over a distance of up to some 400 m on the E flank of the Alainen Rautuvaara hill. The sediments form part of an up to 40 m-thick valley-infill consisting of glacial and fluvial deposits. The Rautuvaara section has earlier been considered as the stratotype for the northern Fennoscandian late Middle and Late Pleistocene (Hirvas, 1991). However, recent dating by OSL indicates that the whole sediment succession was deposited during the Weichselian (Lunkka *et al.*, 2014; Howett *et al.*, 2015).

Late Quaternary stratigraphy

A series of boreholes has been collected from the Sokli basin since 1996 using percussion drilling from the frozen surface of the Sokli wetland (Fig. 1). Coring was performed at three different locations along a 200 m long transect and, at each location, several cores were taken within a few meters distance from each other. Additionally, a 9 m-thick Holocene sediment sequence was

collected from Lake Loitsana using a Russian peat corer from the frozen lake surface. This lake, which occupies a depression associated with a NW-SE trending esker chain, is the only place within the Sokli massif where open-water conditions persist today.

The Sokli and Loitsana sediments have been dated by means of AMS ^{14}C dating on macrofossils of terrestrial plants, TL and IRSL dating, and OSL dating on quartz using SAR dose protocol (Helmens *et al.*, 2000, 2007a, 2007b, 2018; Alexanderson *et al.*, 2008; Shala *et al.*, 2014b; Fig. 1). The latter yielded large standard errors mainly due to small sample sizes, relatively poor luminescence characteristics, and uncertainties in dose-rate determinations. OSL ages on glacio-fluvial and fluvial sediments are, however, in sequence and group according to stratigraphic units. Also, the youngest age determination agrees with ^{14}C dates, and the oldest ages are in line with the TL and IRSL dates. Moreover, the absolute chronology is in agreement with earlier made land-sea comparisons (Helmens *et al.*, 2000, 2007a; Alexanderson *et al.*, 2008).

An up to 9 m-thick, yellowish-brown diatom gyttja deposit, dated to MIS 5e, stretches as a marker horizon near the base of the Sokli basin infill (Fig. 1). The diatom gyttja is underlain by minerogenic sediment of glacio-lacustrine origin. According to prospecting by Ilvonen (1973), the diatom gyttja unit overlies till (MIS 6) that rests on weathered bedrock. The ice-divide zone was situated over the northernmost part of Finnish Lapland during the Penultimate Glacial (MIS 6; Johansson, 1995), which would have allowed for more glacial erosion at Sokli at this time compared to the LGM (MIS 2).

The MIS 5e sediments, which were deposited in an initially deep and stratified lake, are overlain by a several meters thick, minerogenic fluvial deposit. Fossil remains in the upper, more fine-grained portion of latter deposit of MIS 5d age, together with lithology, indicate a braided river pattern. The prolonged infilling of a small oxbow lake, and return to stream channel deposition, are subsequently recorded in an overlying, over 3 m-thick gyttja deposit interbedded with sand and gravel, dated to MIS 5c.

The upper part of the Sokli sedimentary record consists of till interbedded with two more sorted sediment units dated to MIS 5a and early-MIS 3. The glacial lake sediments of early-MIS 5a age are overlain by up to ca. 2 m of gyttja, and this lake sequence can be followed over a distance of at least 100 m (coring locations 1 and 2 in Fig. 1). The glacio-lacustrine sediments of early-MIS 3 age are capped by till.

Material and methods

Lithology and chronology

The MIS 5a deposit, which is highlighted in Figure 1 by a yellow box, occurs at depths of ca. 9-12 m below the surface of the Sokliaapa. The underlying compact diamicton is clast supported in its lower part, whereas a sandy matrix dominates in the weakly stratified upper part. The diamicton is interpreted as basal till possibly overlain by ablation till (Helmens *et al.*, 2000, 2007a). Subsequently, the sediment becomes more sorted and fines-upward to sand. This glacio-fluvial sediment is abruptly overlain by a laminated silt-clay deposit of glacio-lacustrine origin (Helmens *et al.*, 2018). The overlying gyttja deposit is truncated by till in borehole 900, whereas in boreholes B-series and 2/2010, the gyttja becomes increasingly interlayered with sand before turning to sand interbedded with thin organic laminae and then gravel at the top. The gyttja deposit attains its greatest thickness (ca. 2 m) in borehole 2/2010 that is studied here.

A detailed lithological column with LOI to the right, and absolute age determinations to the left, is given in front of the diagrams in Figure 2. The ^{14}C dating results have been presented in Helmens *et al.* (2018) and the OSL datings (which were performed on the B-series borehole; Fig. 1) in Alexanderson *et al.* (2008). The chronology roughly corresponds with MIS 5a around 82 kyr BP (Helmens *et al.*, 2007a; Alexanderson *et al.*, 2008).

Biotic proxy analyses

The MIS 5a deposit in borehole 2/2010 was sliced in ca. 10 cm- (minerogenic sediment) and ca. 5 cm-thick samples (gyttja; clayey sediment below 11.90 m). The majority of samples was analysed for pollen, spores and NPP's (i.e. the palynological analysis) and chironomids. A lower sample resolution was used in the macrofossil, diatom and LOI analyses. The multi-proxy analysis is similar as applied to the sediments of MIS 5e and Holocene age in the Sokli basin and follow the methods described in Salonen *et al.* (2018; palynological analysis) and Shala *et al.* (2014a, b; other analyses). The coring operation is described in Plikk *et al.* (2016). A minimum of 500 diatom valves, 50 chironomid head capsules and 400 terrestrial pollen/spore grains were identified per sample. Percentages of all microfossils encountered in the palynological analysis were calculated based on the sum of terrestrial plant taxa (trees, shrubs, dwarf shrubs, herbs, Pteridophytes). The sample sizes used in the macrofossil analysis varied between ca. 15 (gyttja) and 35 cm^3 (minerogenic sediment), and ca. 5 cm^3 of sediment per sample was analyzed below 11.90 m.

A selection of diatom and chironomid taxa is given in Figure 2A. Pollen, spores, NPP's and macrofossils of plants and zoological taxa (excluding insects) are presented in Figures 2B and 2C, where Fig. 2B combines micro- and macrofossil remains of taxa that occur in aquatic and wetland environments and Fig. 2C combines fossil remains of terrestrial plant taxa. Zonation of the diagrams is based on visual examination of the entire dataset including lithology, following our earlier studies at Sokli (e.g. Helmens *et al.*, 2012). A common zonation is applied to the diatom, chironomid and other aquatic and wetland taxa diagrams (Figs. 2A, 2B). This zonation consists of five local zones, I-1 and -2 and II-1, -2 and -3. The zonation in Fig. 2C (zones I, II, III-a and -b) follows the terrestrial vegetation development. In addition to the multi-proxy analysis performed on core 2/2010, a low-resolution macrofossil analysis was carried out on the MIS 5a deposit in the B-series borehole. Results are given in Table 1. The previously obtained low-resolution pollen data for the MIS 5a deposit in the Sokli basin comes from borehole 900 (Fig. 1; Helmens *et al.*, 2000, 2007a).

It is important to note that in Fennoscandia several plant taxa (e.g. Cyperaceae, *Betula nana*, Ericales) occur as important element in both terrestrial and wetland settings. Herbs for which a distinct wetland habitat could be inferred for parts of our record (e.g. Cyperaceae), as well as herbs in shore settings (e.g. *Rorippa*) or for which the habitat was undifferentiated (e.g. *Thalictrum*), are given in the lower diagram in Fig. 2C ('other herbs'). The macrofossils of e.g. *Carex*, *Salix*, *B. nana* and Ericales, however, which can be assumed to have an overall local wetland source, are shown in the aquatic/wetland diagram of Fig. 2B. It should also be stressed that pollen and spores of plants from nearby, local wetland or shore environments (i.e. azonal vegetation) are often over-represented in the palynological record and may obscure the regional (zonal) vegetation signal in the percentage diagram. Therefore, we begin our environmental reconstruction with an interpretation of lake development and associated azonal vegetation types before reconstructing the regional vegetation history.

Climate reconstruction methods

Plant indicator species

Minimum mean July air temperatures (T_{jul}) are reconstructed from the plant macro- and microfossil records using the approach introduced in Väliranta *et al.* (2015). In this protocol, current plant species distribution data in Finland are linked to measured meteorological data over a T_{jul} gradient from ca. 7.5 to 17 °C. This gradient spans over several bioclimatic zones from hemiboreal, via boreal to subarctic and, therefore, many plant species reach their northern distribution limits within this gradient. Only in the northernmost part of the country, the plant distributions are constrained by altitude-related (orohemiarctic) factors. A unique modern species-specific spatial plant distribution dataset (http://www.luomus.fi/kasviatlas) covers the whole Finland and is subject to continuous botanical surveys. Long-term meteorological climate normal data are readily available. Thus, the plant distribution database can be used to correlate modern species distributions with climate.

Plant indicator species identified in the MIS 5a fossil record, together with their minimum T_{jul}

requirements in Finland, are listed in Table 2. These plant species require a specific minimum T_{jul} in

order to flower and reproduce and have a rather sharp northern distribution limit. For each species,

we use an interpolated T_{jul} over a 10 × 10 km grid cell, and we analysed several grid cells containing

species occurrences along the current northern distribution boundary. A median and mean July

temperature range, i.e. the lowest and highest temperature value along the species-specific

distribution boundary in the grid cells, are given in Table 2 and Figure 3B.

Pollen-based climate reconstruction

The pollen-based climate reconstruction method, similar as the chironomid-based reconstruction

discussed below, makes use of the transfer function approach (Birks et al., 2010). It uses a modern

calibration set linked to current meteorological data. The calibration set consists of

pollen/chironomid assemblages analyzed in surface sediment from a series of lakes situated along a

gradient that covers changes in the parameter of interest, here T_{jul}. The established relationship is

used in combination with the fossil data to model past changes in T_{jul}.

The pollen-based T_{jul} reconstruction method applied here generally follows Salonen *et al.* (2018). The

latter presented a reconstruction based on the MIS 5e pollen sequence at Sokli. The climate

reconstruction uses a modern calibration dataset consisting of 807 European lakes, derived from the

European Modern Pollen Database (Davis *et al.*, 2013), with modern climate data extracted for each

sample location. For further details about this calibration dataset see Salonen *et al.* (2019). We fitted

pollen-T_{jul} calibration models to the calibration data using six generally well-performing (in modern

cross-validation experiments; Salonen *et al.*, 2018, 2019) statistical approaches (weighted averaging

(WA); weighted averaging-partial least squares (WA-PLS); maximum likelihood response surfaces

(MLRC); modern analogue technique (MAT); random forest (RF); boosted regression trees (BRT)).

The median of the six-method ensemble was calculated to summarize the individual reconstructions.

Furthermore, to assess the reliability of the paleo-climate reconstructions beyond the cross-

validated errors, we calculated the compositional distance (squared chord distance; Overpeck *et al.*, 1985) to the closest-matching modern pollen assemblage for each fossil sample. Results are presented in Figure 3A.

Chironomid-based climate reconstruction

The chironomid-based T_{jul} reconstruction was performed using the Finnish latitudinal (60-70 °N) calibration model presented in Luoto (2009). The model is specifically designed for shallow (< 7 m) boreal to sub-arctic sites. The calibration set has a temperature range of 11.3-17.1 °C and it includes 82 sites and 110 chironomid taxa. The model is constructed using the WA-PLS technique and has a jackknife cross-validated coefficient of determination (R^2_{jack}) of 0.78 °C and a root mean squared error of prediction (RMSEP) of 0.72 °C. Estimated standard errors of prediction (eSEP), i.e. sample-specific errors in the reconstructions, were established using bootstrapping with 999 iterations. Closest modern analogues of the fossil samples in the calibration sets were assessed using the modern analogue technique (MAT) with squared chi-square distance as a dissimilarity coefficient and a 5-percentile threshold (minDC) for poor/good analogues. Results are presented in Figure 3C.

Environmental reconstructions

Successions in aquatic and telmatic ecosystems and lake development

Local zone I (depth interval 12.15-11.00 m)

Local zone I corresponds to over 1 m of minerogenic sediment (organic content measured by LOI varies between 3 and 5 %; Fig. 2) found at the base of the MIS 5a sequence. This sediment accumulated in the Sokli Ice Lake that developed during deglaciation between the retreating margin of the Fennoscandian Ice Sheet in the NW and higher terrain to the SE (Johansson, 1995; Helmens *et al.*, 2009; Shala *et al.*, 2014a). A selection of fossil remains from the glacial lake sediment has been

earlier presented, and compared with fossil assemblages found in similar sediment of early-MIS 3 and -Holocene age in the Sokli basin, in Helmens *et al.* (2018).

Local zone I-1 (12.15-11.80 m)

The lower, upward-fining sequence of sands and silts grading into rhythmically laminated silts and clays (local zone I-1) was deposited in a deep and expanding glacial lake and contains few macrofossils and fossil head capsules of chironomids. The cladoceran *Daphnia* (water-flea; recorded by ephippia), the pioneering, colonial green alga *Botrycoccus braunii*, and the bryophyte *Sphagnum* (spores) are among the few taxa that are well-represented in the fossil record other than diatoms (Fig. 2B).

The diatom assemblage (Fig. 2A) is dominated by Fragilariaceae (predominantly *Staurosira construens*) and *Aulacoseira*. Fragilariaceae species are generally considered to be opportunistic and pioneering due to their wide range of ecological preferences (Smol, 1983; Anderson, 2000). They are favoured by relatively high alkalinity (Battarbee, 1986) and are often found in lakes that have some sort of disturbance such as proglacial environments (Bigler *et al.*, 2003; Risberg *et al.*, 1999). The encountered planktonic *Aulacoseira* species (*A. ambigua*, *A. subarctica*, *A. alpigena*) are all heavily silicified and indicate a high influx of silica into the lake and enhanced levels of turbulence to keep these diatoms suspended in the water column. The laminated silts in uppermost part of local zone I-1 show increased representations of periphyton (taxa attached to plants) *S. construens* var. *binodis*, *Pseudostaurosira robusta* and *Navicula scutelloides* and, in combination with LOI values rising to 5 %, probably reflect an extension in the lake's littoral zone. Relatively nutrient-rich conditions (in particular phosphate) are suggested by eutrophic *Stephanodiscus* species (*S. neoastraea*, *S. medius*) and *A. granulata* (Anderson, 2000).

Local zone I-2 (11.80-11.00 m)

The upper 80 cm of silty glacial lake sediment was deposited in a smaller and shallower lake (local zone I-2). This lake stage developed after the opening of a spillway along the retreating ice-margin that lead to partial drainage of the Sokli Ice Lake. The silt deposit shows laminae of varying grain-sizes (clay to fine sand) and thicknesses and, together with the appearances of stream-inhabiting chironomid taxa (e.g. *Eukiefferiella*, *Rheocricotopus*; not shown in the diagram), suggest inflow of running water close to the coring-site. The fossil remains of the soil fungus *Glomus* (HdV-207; van Geel *et al.*, 1989), abundant fragments of bryophytes and small organic bits, and pieces of wood, were probably transported from the catchment/lake surroundings by running water as well. Statoblasts of *Fredericella* show high abundances in the lowermost part of local zone 1-2. This bryozoan was identified as *F. indica* in the early-MIS 3 glacial lake sediment (Helmens *et al.*, 2017b) and its occurrence might be favoured by wave action (Økland and Økland, 2001) and/or stony shores with sparse aquatic vegetation (Økland and Økland, 2005). Macrophytes that are recorded in low abundances in the silt deposit include *Callitriche hermaphroditica*, *Myriophyllum* and narrow-leaved *Potamogeton*.

Local zone I-2 is characterized by a rich chironomid assemblage (Fig. 2A). The assemblage is dominated by the deep-water taxa *Conynocera oliveri*- and *Chironomus anthracinus*-types. Both taxa also have an affinity for sediment load (Axford *et al.*, 2009; Luoto and Sarmaja-Korjonen, 2011). The littoral taxon *Tanytarsus pallidicornis*-type is presently common in the sublittoral and littoral zones of boreal lakes mostly found living among *Phragmites* stands (Luoto, 2010). The occurrences of *C. anthracinus-, Procladius, Endochironomus albipennis-, T. pallidicornis-, T. mendax-, Polypedilum nubeculosum-, Cladotanytarsus mancus-, Microtendipes pedellus-* and *Chironomus plumosus*-types suggest meso- to eutrophic water conditions. The latter is supported by the recording of the macro-alga *Nitella* (oospores) and the diatom taxa *S. medius* and *S. minutulus*.

The sediment becomes sandier in the uppermost part of local zone I-2 and, together with the fossil record, suggest a further shallowing of the glacial lake accompanied by an extension in the littoral zone. The littoral diatom taxon *Staurosirella pinnata* shows a sharp increase in percentage values and macrofossils of wetland plants (*Carex, Salix*, *B. nana*) and the aquatic plant *Callitriche hamulatea* are found. Also, pollen of sedges (Cyperaceae) increase in percentage values (Fig. 2C). The fossil record in the sandy sediment is further characterized by enhanced percentages for the diatom species *Aulacoseira granulata* var. *angustissima*. Together with the recording of *Amphora libyca* and *S. leptostauron*, this diatom assemblage indicates alkaline waters with high Ca-concentrations (Gómez *et al.*, 1995; Jones and Birks, 2004).

Local zone II (11.00-8.90 m)

The Sokli Ice Lake drained at the transition from local zone I to II and lacustrine sedimentation continued in a relatively small depression within the Sokli basin. Fragilariaceae continue to show mass-abundances throughout local zone II. This might be related to an increased influence of the local carbonatite bedrock on the lake water chemistry in the now greatly reduced catchment.

Local zone II-1 (11.00-10.15 m)

Local zone II-1 records a dynamic lake environment with rapid turn-over of aquatic and telmatic communities.

The lowermost samples indicate shallow water conditions. Spores of *Equisetum* and pollen of sedges and *Salix* are well-represented in the fossil record, and it is possible that the enhanced pollen percentage values for Ranunculaceae, Rosaceae and Apiaceae are related to a local wetland or shore habitat as well (Fig. 2B-C). Macrofossil remains of wetland elements (*Salix, Carex, Ranunculus* sect. *Batrachium*) and aquatic taxa (*Callitriche hermaphroditica*, *C*. cf *cophocarpa*, *Potamogeton*) are found. Open-water is indicated by statoblasts of the bryozoa *Plumatella* and *Cristatella mucedo.* *Pediastrum boryanum* var. *pseudoglabrum*, a green alga associated with shallow, macrophyte-rich,

eutrophic environments (Bradbury and Winter, 1976; Cronberg, 1982), shows also enhanced percentage values.

Following the initial lake stage with shallow waters, the deep-water taxon *Tanytarsus lugens*-type appears with high occurrences. The chironomid assemblage in the organic bearing silt layer further includes a variety of meso-eutrophic taxa (*E. albipennis*-, *P. nubeculosum*-, *C. mancus*-, *C. plumosus*-types). This indicates that nutrient-rich conditions continued to prevail. *Cymbella ehrenbergii*, a diatom species found in calcareous lakes and slow-flowing rivers (Elliott *et al.* 2011), shows enhanced percentages as well.

Tanytarsus lugens has a relatively high oxygen demand and its sudden decline near the base of the finely laminated gyttja is probably related to increased anoxia. The latter decreases bioturbation and this allows preservation of lamina in the sedimentary record. *T. lugens* is replaced by high numbers of *Conynocera ambigua*, an oligo- to mesotrophic species common in clear alkaline waters. Compared with *P. boryanum* var. *pseudoglabrum*, which was recorded in the basal organic silts, the alga *P. integrum* is associated with oligotrophic and cool waters (Komárek and Jankovská, 2001; Sarmaja-Korjonen *et al.*, 2006).

The upper part of the finely laminated gyttja bed shows *C. ambigua* being replaced, as dominant taxa, by *P. sordidellus*- and *Cricotopus intersectus*-types in the chironomid assemblages. Both are related to macrophyte abundances. Aquatic plants have become well-represented in the fossil record and include abundant leaf remains of narrow-leaved *Potamogeton* (*P. pusilus/pectinatus/rutilus*, *P. berchtoldii*) and pollen of *Potamogeton*, *Callitriche* and *Myriophyllum spicatum*-type. The overall increase in percentage values for the diatom taxon *Staurosira construens* var. *venter* probably reflects its periphytic habitat preference as well. *P. pusilus* and *P. pectinatus* are presently recorded in mesohaline waters.

The typical littoral chironomid type *C. intersectus* attains highest abundances in the upper portion of local zone II-1 and, together with the appearances of macrofossil remains of *Myriophyllum*,

Ceratophyllum (see zone II-2) and *Carex*, most probably reflect an extension in the lake's littoral zone. The cyanobacteria (blue-green alga) *Gloeotrichia*-type is recorded, as well as the diatom *Epithemia sorex,* an epiphytic taxon which has cyanobacterial endosymbionts that are capable of nitrogen-fixation (Marks and Power, 2001), such as *Gloeotrichia*. The imbalance in P/N ratio might be the result of increased nutrient loading connected with terrestrial erosion. According to Van Geel *et al.* (1996), *Gloeotrichia echinulata* depends on sediment P rather than epilimnic P. Increased percentage values for *S. leptostauron*, a diatom taxon often found growing attached to sediment grains, and rheophilic diatoms (e.g. *Meridion circulare*), suggest a closer proximity to inflow of running water. Alkaline lake water conditions are indicated by *S. construens* var. *subsalina* and *S. leptostauron.*

Local zone II-2 (10.15-9.35 m)

Characteristic for local zone II-2 are *Ceratophyllum* leaf spikes (HdV-137; van Geel *et al.*, 1989) identified in the pollen analysis, which are particularly abundant in the lower part of the local zone, and high percentage values of the green alga *Spirogyra* (Zygnemataceae) in the local zone's upper part. Two species of the aquatic plant *Ceratophyllum* presently occur in Finland, *C. demersum* and *C. submersum*. The latter has only few localities along the southern coastline, which have established during the last two decades. *C. demersum* occurs in shallow, eutrophic, oligo- to mesosaprobic water bodies (i.e. exclusively oxidizing to partly reducing decomposition) (Westhoff and den Held, 1975). It tolerates highly polluted waterways where e.g. human-induced eutrophication has led to impoverishment of the flora (Westhoff *et al.*, 1981). *Spirogyra* is represented in the fossil record by four types (HdV-130, -132, -210, -315; Pals *et al.*, 1980; van Geel *et al.*, 1983, 1989; van der Wiel, 1983) and is characteristic of stagnant, shallow, meso-eutrophic freshwaters (van Geel and Grenfell, 1996). Local zone II-2 is further characterized by relatively high abundances of *Orthocladius oliveri*- and *Dicrotendipes nervosus*-types, chironomid taxa also related to shallow, eutrophic waters.

Other macrophytes that are recorded include *Myriophyllum spicatum*-type (including *M. verticillatum* and *M. sibiricum*), *M. alterniflorum*, narrow-leaved *Potamogeton compressus*, *Sparganium*, *Nuphar*, *Elatine triandra, Callitriche hermaphroditica* and *Hippurus. Paratanytarsus penicillatus*-, *Cladotanytarsus mancus*- and *Cricotopus cylindreacus*-types are chironomid taxa common in meso- to eutrophic waters, whereas *Zalutschia zalutschicola* is a humic indicator (Luoto, 2013).

An extension in the wetland zone during local zone II-2 is indicated by high spore percentage values of *Equisetum* accompanied by conductive tissue (HdV-217; van Geel *et al.*, 1989), bryophytes spores (HdV-340; van Geel *et al.*, 1989), the recording of *Typha* and *Selaginella selaginoides*, and an overall increase in Cyperaceae pollen. The latter parallels strong increases in fern spores (*Dryopteris*-type, *Athyrium*, *Pteridium*), suggesting an extension/close proximity of wetland or shore habitats as well. *Tilletia sphagnii* (HdV-27; van Geel, 1976) and *Ustulina deusta* (HdV-44; van Geel, 1976) are fungi, the latter growing on wood substrate. The extension in the littoral was accompanied by a further encroachment of running water as indicated by increased values of rheophilic diatoms (e.g. *Diatoma mesodon*) and the occurrence of the semi-terrestrial chironomid *Limnophyes.*

Epiphytic diatom *Epithemia adnata* shows enhanced values in the uppermost part of local zone II-2 and, like *E. sorex*, is capable of N fixation. It is found in neutral to high pH environments. *Cocconeis placentula, Rhopalodia gibba* and *Amphora libyca* are all alkaliphiles species.

Local zone II-3 (9.35-8.90 m)

The sandy lithology of local zone II-3, and the fossil content, indicate an advanced stage of infilling and overgrowing of the lake (terrestrialisation), and an increased influence of running water close to the coring-site. Macrofossils of a variety of wetland plants (*Carex, Salix*, *B. nana, Juncus*, *Eriophorum, Trichophorum*, *Ranunculus* sect. *Batrachium*) and woody pieces are abundantly present, and *Glomus* returns in the fossil record. *Staurosirella pinnata* is known to tolerate rapidly changing environments

and often dominates shallow waters with sandy substrates (Haworth, 1976; Jones and Birks, 2004). *S. lapponica* indicates shallow, and possibly less productive, conditions.

Regional vegetation development

Zone I (depth interval 12.15-11.00 m)

Pollen of the shrub *Betula nana* were separated from pollen of the tree *B. pubescens/pendula* using a combination of size and morphological characteristics as described in Terasmaë (1951). The similarity between the pollen curves of *B.* undifferentiated and *B. nana* in the pollen diagram (Fig. 2C) indicates that the former probably represents *B. nana*. This means that *B. nana* is represented in the pollen assemblage of zone I by percentage values of up to ca. 20-30 %. Dwarf shrubs (Ericales) and lycopods (including *Diphasiastrum*, *Huperzia selago*) are also well-represented. Together with *B. pubescens/pendula* pollen reaching values of ca. 40 %, and *Pinus* pollen to ca. 20 %, this pollen assemblage suggests the presence of low-arctic shrub tundra vegetation in close vicinity to the birch forest ecotone (Prentice, 1978). The latter is supported by macrofossil findings of tree birch in the glacial lake sediment, both in the 2/2010 (Fig. 2C) and B-series boreholes (Table 1). In addition, larch trees were present. *Larix* is generally very poorly represented in the fossil record due to short-distance dispersal and poor preservation (Gunin *et al.*, 1999; MacDonald *et al.*, 2000) and even low percentage values can be taken as evidence for its local presence. In contrast, the pollen of *Pinus* as well as *Picea* are most probably the result of long-distance transport (Aario, 1940). Grasses (Poaceae) are well-represented in the pollen record from the glacial lake sediment, both during early-MIS 5a and -MIS 3 and the early-Holocene (Helmens *et al.*, 2018). High amounts of pooid (grass) phytoliths in the latter records, and the recording of Poaceae fuits in the early-MIS 5a deposit in borehole B-series (Table 1), point to a local, littoral/shore habitat and indicate that Poaceae are probably over-represented in the glacial lake pollen records.

Zone II (11.00-10.15 m)

The proportion of *B*. *pubescens/pendula* pollen sharply increases at the base of the gyttja deposit and records the establishment of birch forest in the Sokli region (zone II). *Larix* continues to be registered. *Lycopodium clavatum* is relatively well-represented during zone II as well as in pollen samples from surface lake sediments in the present-day birch and pine-birch forests (Seppä *et al.*, 2004).

Zone III (10.15-8.90 m)

Pinus pollen show a rising trend during zone III, and *Pinus* stomata are recorded, simultaneously when total tree pollen fall. Since the latter is due to increasing representations of sedges and ferns in the lake's littoral zone (see above), this does not reflect an opening of the regional vegetation. The start of rising *Pinus* pollen percentage values at the base of zone III-a coincides precisely with the transition to shallow water conditions in the Sokli basin recorded at the base of local zone II-2. It is possible that the increased representation of pine in the regional forest contributed to the lake shallowing, due to increased evapotranspiration and reduced run-off. In the B-series borehole, pollen of Cyperaceae reach percentages of 40 % (Helmens *et al.*, 2000), and *Carex* seeds dominate the macrofossil record (Table 1), indicating even shallower lake conditions at this site compared to the location of the 2/2010 borehole.

Pollen of *Pinus* reach values of over 40 % during zone III-b, after excluding both sedges and ferns from the pollen sum, and indicate the establishment of pine-birch forest at Sokli. *Alnus* is probably represented in a moist habitat around the lake, *Larix* and *Juniperus* are present, whereas pollen of *Quercus*, *Ulmus*, *Corylus* and *Fraxinus* are probably the result of long-distance transport.

Climate development

Plant indicator species- inferred T_{jul}

Plant macrofossil remains are scarce in the glacial lake sediment at the base of the MIS 5a lake sequence. In the overlying, organic-bearing deposit, a variety of aquatic plants (*Ceratophyllum, C. cophocarpa*, *P. compressus*) indicate minimum T_{jul} values of around 13.5-14 °C, with *E. triandra* and the wetland element *Typha* suggesting minimum values up to around 15-15.5 °C (Table 2; Fig. 3B).

Pollen assemblage - inferred T_{jul}

The pollen-based T_{jul} reconstruction (Fig. 3A) is characterized by a considerable variation between the general temperature levels during MIS 5a reconstructed by the six different pollen-climate calibration models. The disagreement between methods is in sharp contrast with the prior application of an identical ensemble reconstruction approach to the MIS 5e pollen sequence at Sokli (Salonen *et al.*, 2018). A likely contributor to the comparatively large spread in T_{jul} values reconstructed by the model ensemble for MIS 5a (Fig. 3A-2) is the worse quality of modern analogues found in the modern calibration dataset. While for MIS 5e the analogue quality was excellent for major part of the sequence (i.e. even better than for late-Holocene pollen samples from Lake Loitsana; Salonen *et al.*, 2018), for the MIS 5a pollen samples the analogue distances are typically 2–3 times larger than during the late-Holocene. Modern analogues for the MIS 5a fossil samples with best analogue quality are found from N Fennoscandia, somewhat north of the location of Sokli (Fig. 3A-1).

The general poor-fit between the MIS 5a fossil and modern calibration samples are probably due to the character of the MIS 5a lake, i.e. a relatively small and shallow lake with an extensive littoral zone. In contrast, a large open water body with a fringe of wetland prevailed in the Sokli basin throughout major part of MIS 5e. Particularly pollen of sedges (Cyperaceae) and spores of ferns (*Dryopteris*-type, *Athyrium*) show high and increasing percentage values (Fig. 2C) in concordance

with an extension in the littoral (local zones II-2 and II-3; Figs. 2A-B) and these taxa were excluded from the pollen sum in the T_{jul} reconstruction. Nevertheless, there are indications that other herbs and shrubs (*Salix*, Poaceae, Ranunculaceae, Roasaceae, Apiaceae), that were not excluded from the sum, had a local wetland/shore habitat as well and, as such, can be expected to be over-represented in the pollen record and contribute to a poor analogue fit. Furthermore, *B. pubescens/pendula* pollen percentage values reach 70-80 % in the birch forest assemblage of zone II, when applying a sum without sedges and ferns, i.e. greatly exceeding means of ca. 30-35 % in the modern calibration data from Finland and Russia (Salonen *et al.*, 2012). This might be an additional factor leading to poor modern analogues. The high percentages for *B. pubescens/pendula* in the early part of the MIS 5a vegetation development might reflect the strong pioneer character of *Betula* spp., i.e. producing abundant, wind-dispersed fruits, and revealing rapid reproductive rates, fast growth rates and a young reproductive-maturity age (Birks, 1986).

In Fig. 3A-3, the median of the six-method ensemble based on all taxa (blue line) is compared with the median shown in Fig. 3A-2, i.e. produced by applying a pollen sum without sedges and ferns (red line). The largest difference in reconstructed T_{jul} is shown in zone III-b with pine-birch forest in the Sokli area, with the limited assemblage showing the highest T_{jul}, reaching near present-day values (13 °C). This value agrees with a minimum T_{jul} of 12 °C for pine forest in modern-day N Fennoscandia (Väliranta *et al.*, 2015). The low T_{jul} inferred by the full taxa assemblage for zone III-b can be ascribed to the low temperature optimum for Cyperaceae in the calibration dataset (Salonen *et al.*, 2012; see also Salonen *et al.*, 2013).

Chironomid assemblage - inferred T_{jul}

The chironomid-inferred T_{jul} reconstruction (Fig. 3C) shows overall increasing values from 12.7 °C at the base of the MIS 5a lake sequence to 15.8 °C at the top, with constant sample-specific errors of 0.7-0.9 °C. In general, the early part of the temperature record has high variability, but the mid-part is more stable (14-15 °C). Typical for pre-Holocene records, most samples have poor modern

analogues according to MAT. Despite the poor fit between the fossil chironomid and modern calibration samples, all fossil samples had good coverage of taxa present in the calibration dataset with at least 94 % of the fossil taxa present in the calibration data.

The low T_{jul} reconstructed near the base of the glacial lake deposit (base of local zone I-2), and in the overlying organic-bearing silt bed (lowermost part of local zone II-1), appear to be driven by the deep-water taxa *Corynocera oliveri-* and *Tanytarsus lugens*-types (Fig. 2A), which have temperature optima at 12.8 and 13.5 °C, respectively, in the modern calibration set. These taxa probably occurred in the cold profundal of the MIS 5a lake and therefore might reflect water temperature instead of air temperature. Although *C. oliveri-* and *T. lugens*-types are classical cold indicator taxa (Brooks, 2006; Self *et al.* 2011), both are also typical pioneers in coarse substrates (Axford *et al.*, 2009; Luoto and Sarmaja-Korjonen, 2011).

Corynocera ambigua is one of the few other cold temperature chironomid taxa (optimum 13.7 °C) encountered in the MIS 5a sediment sequence. It shows overall high occurrences in the mid-part of the lake sequence (local zones II-1 and II-2) with more stable T_{jul} inferences. The modern distribution of *C. ambigua* in Finnish lakes is related to cold oligo-mesotrophic waters, but it is known to have a complex ecology (Brodersen and Lindegaard, 1999). It is reported to dominate the assemblage in temperate lakes as well (Brodersen and Lindegaard 1999), and in the Holocene record from Lake Loitsana, high numbers of *C. ambigua* have been related to macrophyte density, particularly of *Myriophyllum* (Shala *et al.*, 2014b). *Myriophyllum* is also well-represented in the macrofossil record of local zones II-2 (Fig. 2B), but the high abundances of *C. ambigua* in the early half of local zone II-1 might be related to clear alkalinity water conditions.

The mid-part of the MIS 5a lake sequence is further characterized by a large number of intermediate- to warm-water chironomid taxa, including *Microtendipes pedellus-* (optimum T_{jul} at 14.6 °C), *Psectrocladius sordidellus-* (14.7 °C)*, Cricotopus intersectus-* (15.2 °C), *Cladotanytarsus mancus-* (15.4 °C), *Cricotopus cylindreacus-* (15.6 °C) and *Chironomus anthracinus*-types (15.7 °C),

suggesting warm summers, although the relatively high occurrences of *P. sordidellus*- and *C. intersectus*-types might be driven by habitat (affinity to macrophyte abundance) as well. The apparent increase in T_{jul} in the uppermost part of the record is probably caused by decreasing occurrences of *C. ambigua* as the lake became increasingly shallow and eutrophic.

Because of the influence of habitat preference on the chironomid assemblages, the trend in T_{jul} as well as the absolute T_{jul} values shown in Fig. 3C should be treated with caution. Nevertheless, the predominance of intermediate to warm chironomid taxa possibly indicates relatively warm summers. We used the calibration model by Luoto (2009) to accommodate for the overall shallow nature of the MIS 5a lake. However, the temperature range of this calibration set is relatively short and was recently extended at the cold end from 11.3 to 7.9 °C (Luoto *et al.*, 2014a, 2014b). Based on the new model, the T_{jul} optima for the intermediate- to warm-water chironomid taxa are on average ca. 1 °C lower. They provide a T_{jul} range in the order of 13 to 15 °C, which is in line with the July temperature estimates inferred from the plant indicator species.

Discussion

Environmental and climate developments at Sokli during MIS 5a

The fossil remains analyzed in the lake deposit of MIS 5a age in the Sokli basin, including pollen, spores, NPP's, macrofossils, diatoms and chironomids, record with great sensitivity the lake history and associated, successional developments in aquatic and telmatic ecosystems. Characteristic are the alkaline and nutrient-rich lake water conditions which resulted from a combination of factors including: 1) the local carbonatite bedrock; 2) rapid leaching of carbonates and other soluble minerals from surface soils shortly after deglaciation (Engstrom *et al.*, 2000; Helmens *et al.*, 2018); 3) sudden lake volume reductions (morphometric eutrophication; Hofmann, 1998), such as following the drainage of the Sokli Ice Lake (Shala *et al.*, 2014a); 4) lake shallowing due to infilling; and 5)

inflow of running water and sediment close to the coring-site. Relatively high sedimentation rates, suggested by overall low LOI values (Korhola and Weckström, 2004), allowed an exceptional detailed reconstruction of the development of the Sokli Ice Lake and subsequent infilling of a relatively small and shallow lake confined to the Sokli basin.

The regional vegetation development that is recorded, following the moment of deglaciation, is typical for the early half of an interglacial at the latitude of Sokli. It is characterized by low-arctic shrub tundra being replaced by pioneer birch forest and then pine-dominated boreal forest. The latter vegetation is similar as recorded in the Lake Loitsana sequence at the start of the mid-Holocene (Shala *et al.*, 2017). The late part of the MIS 5a warm stage is missing in our records due to lake infilling.

Our study shows the importance of validating quantitative climate estimates inferred from fossil remains in lake sediments against the lake's own history. The multi-proxy based reconstruction of lake development shows that the chironomid assemblages in the MIS 5a lake deposit are strongly driven by non-climatic factors including changes in water depth, lake water geochemistry (alkalinity, eutrophication) and macrophyte abundances. Therefore, the trend as well as the absolute values of the chironomid based-T_{jul} reconstruction should be treated with caution. Nevertheless, most taxa are intermediate to warm indicators and show T_{jul} optima in the range of 13 to15 °C, in line with the T_{jul} estimates inferred from the aquatic and wetland plant indicator species. The present-day distribution of the latter species is regulated by temperature, not edaphic factors or water chemistry (Väliranta et al., 2015 and references therein). For example, the distribution of *Typha* is currently restricted to S Finland, and this taxon is not present at Sokli today, even though suitable habitats with moist, nutrient-rich soil are extensively available (Shala et al., 2017). However, since the presence of macrofossils in lake sediments strongly depend on taphonomic factors (e.g. distance to shore), the plant indicator species-inferred climate record is discontinuous. Finally, the expansion in the littoral caused by the infilling of the MIS 5a lake hampers the modelling of the pollen

assemblage-climate relationship. The wetland element Cyperaceae is over-represented in the pollen record from the upper part of MIS 5a lake deposit and, since Cyperaceae have some of the lowest temperature optimum in the calibration set (corresponding to tundra conditions), results, if uncorrected for, in an under-estimation of T_{jul}. By applying a pollen sum that excludes Cyperaceae as well as ferns, the pollen-based T_{jul} reconstruction reaches the present-day value of 13 °C in agreement with a minimum T_{jul} of 12 °C for pine forest in modern-day N Fennoscandia.

Despite the shortcomings in the climate reconstructions, there is evidence for warmer-than-present summers during early-MIS 5a. Warm, insolation-forced summers are also reported for the early-Holocene in northern Fennoscandia (Kullman, 1999; Bigler *et al.*, 2003; Luoto *et al.*, 2014b; Väliranta *et al.*, 2011, 2015; Paus and Haugland, 2017; Shala *et al.*, 2017). The apparent lag in terrestrial vegetation response, both during early-MIS 5a and -Holocene, might be due to time needed for slow soil forming processes (e.g. Väliranta *et al.*, 2015; Helmens *et al.*, 2018), although the establishment of pioneer birch vegetation upon deglaciation might itself have delayed the development of boreal forest. Competition of niches (Giesecke and Bennett, 2004) is mentioned by Väliranta *et al.* (2011) as a possible factor explaining the considerable time-lag by up to 3000 yr between the first macrobotanical and/or stomata finds of spruce and the establishment of closed (mixed) spruce forest in NE European Russia during the early-Holocene. Birch pollen percentage values rise earlier, and values are higher and always exceed the threshold PAR (pollen accumulation rate) value for open birch forest (Seppa and Hicks, 2006), than do spruce pollen records at the Russian sites. Our chronology for the MIS 5a deposit does not allow the calculation of PAR, but PAR values for the early-Holocene pioneer birch forest at Loitsana also greatly exceeds those for the present-day birch forest in N Europe (J.S. Salonen, personal communication).

The Last Interglacial Complex (MIS 5) in the Sokli basin and wider implications

The lake deposits of MIS 5e, 5c and 5a age in the Sokli basin each have their own unique signature in the basin's Late Quaternary stratigraphy (Fig. 1). The successive developments in aquatic and terrestrial ecosystems depicted by their rich fossil records indicate that fossil remains occur *in-situ* and are not the results of redeposition of older material as suggested in Forsström (1990). The distinctly different lake histories inferred from the sediment and fossil records also show that there is no evidence for a domino-like stacking of glacio-tectonically upthrusted interglacial sediment wedges as suggested by Gibbard (written com., 2014) in Otvos (2015). The near continuous sedimentary sequence of MIS 5 age in the Sokli basin provides an exceptionally long environmental and climate record for N Europe, i.e. a region where deposits or fossil records dated to either of the sub-stages of MIS 5 (MIS 5e, 5d, 5c, 5b, 5a) are rare. The data presented here for MIS 5a, and the earlier-published data for MIS 5c and MIS 5e, fully support Helmens (2014) in defining MIS 5 at Sokli as the Last Interglacial Complex, placing the start of the Last Glacial at the base of MIS 4 at ca. 70 kyr BP.

The up to 9 m-thick diatom gyttja of MIS 5e age at Sokli was deposited in a lake that was initially deep and stratified. A large open water body persisted until the last stages of infilling of the lake. A rich algal record (diatoms, green algae; Plikk et al., 2016) characterizes the lake deposit. The sandy gyttja deposit of MIS 5c age accumulated in a small oxbow lake that remained flooded throughout its infilling process. An exceptionally abundant macrofossil record of plants and insects (Engels *et al.*, 2010; Helmens *et al.*, 2012) depicts the different stages of terrestrialisation of the lake and return to stream channel deposition. Although macrofossils are not as abundant as in the MIS 5c gyttja, the fossil record in the lake deposit of MIS 5a age is diverse and traces in detail the development of the Sokli Ice Lake and subsequent infilling of a relatively small and shallow lake confined to the Sokli basin (this study). It is likely that the waterlogged depression in which the gyttja of MIS 5a age deposited formed due to compression of the older sediments under the weight of the

Fennoscandian Ice Sheet during the MIS 5b glaciation. A fluvial deposit of MIS 5d age separates the MIS 5e and 5c gyttja deposits (Fig. 1). The terrestrial vegetation developments during the warm stages of MIS 5 were similar as recorded for the Holocene in the Sokli basin (Shala, 2014). The vegetation succession starts with the replacement of pioneer birch vegetation by pine-dominated boreal forest. The establishment of spruce is recorded in the late-Holocene and late-MIS 5c (Helmens *et al.*, 2012). The presence of spruce is detected early during MIS 5e and *Picea* pollen percentages continuously rise through the MIS 5e lake deposit to a value of 20 % (Salonen *et al.*, 2018). MIS 5e further stands out by the local presence of *Corylus*; hazel reaches its current N limit at over 500 km S of Sokli. Only the early half of the interglacial vegetation succession is recorded for MIS 5a. Summer temperatures exceeding present-day values are inferred for the early- and mid-Holocene (Shala et al. 2017) and all three warm MIS 5 sub-stages (Väliranta *et al.*, 2009; Engels *et al.*, 2010; Plikk *et al.*, 2018; Salonen *et al.*, 2018), whereas warmer-than-today winters are additionally reconstructed for MIS 5e (Salonen *et al.*, 2018).

Similar as at Sokli, MIS 5 has been defined as the Last Interglacial Complex in SW-central Europe (Woillard, 1978; Turon, 1984). Bolikhovskaya and Molodkov (2014) also report the persistence of interglacial climate conditions until the end of MIS 5a for NE-central Europe. The latter results agree with pollen records from loess-palaeosol sequences on the E European Plain, and a mollusc-based ESR (electron spin resonance) chronostratigraphy for the continental margin of N Eurasia, indicating that during most of MIS 5 the vegetation cover in E Europe has evidently been of interglacial character (Molodkov and Bolikhovskaya, 2009, 2010). MIS 5c and 5a have been defined as the Brørup respectively Odderade Interstadials of the Last Glacial in the NW European mainland stratigraphy. The interstadials show mainly boreal forest compared to temperate forest during the Eemian Interglacial (MIS 5e). Particularly winter temperatures are reconstructed to well-below present-day values in NW-central Europe during MIS 5c and 5a (Kühl *et al.*, 2007) compared to minor winter temperature depressions in the east (Šeirienė *et al.*, 2014). The overall warm conditions during all three sub-stages of MIS 5 on the European mainland can be ascribed to higher-than-

present summer insolation (Berger and Loutre, 1991), with possible feedback mechanisms causing the strong decrease in winter temperature in NW-central Europe during MIS 5c and 5a (Šeirienė *et al.*, 2014).

Finally, the warm MIS 5c and 5a interglacial conditions at Sokli, i.e. the near-central area of Fennoscandian glaciation, preclude the persistence of any significant ice mass in Fennoscandia during MIS 5c and 5a. This is in agreement with data from S Europe where speleothem encrustations in coastal caves on the island of Mallorca indicate a sea-level highstand that was slightly higher-than-today, and only slightly lower than the MIS 5e sea-level, during late-MIS 5a (Dorale *et al.*, 2010). The data from Mallorca is consistent with a number of relative sea-level estimates from tectonically stable locations around the world for MIS 5a.

Acknowledgements

Author Contributions

K.H. conceived the study and wrote the manuscript, with input from all authors. C.K., N.K., T.L. and M.V. performed proxy analyses, and T.L. and J.S.S. made quantitative climate reconstructions.

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Tables

Table 1. *Macrofossils encountered in the MIS 5a deposit in borehole B-series. Fossil remains are expressed as concentrations (amounts/5-15 cm^3) or as presence (+) to high abundances (+++).*

Depth in meter, lithology	Woody frag-ments	*Salix* bark, bud, leaf	Fungi scle-rotia	Poa-ceae fruit	*Ro-rippa* seed	cf. *Ranun-culus* seed	*Carex* seed	Organic bits	Mixed bryo-phyte remains	*Equise-tum* remains	*Ranun-culus* sect. *Batra-cium* seed	Tree *Betula* seed, catkin scale	*Betula* seed	*Betula* bark, leaf remains
9.40 organic-rich sand	+++	+	2	1			7		++		1	1		+
9.68 gyttja							15	+++	++	+				
9.82 minerogenic glacial lake sediment	++						2					1		+
10.41 ,,	++	+	1	6	1	2	1					2		
10.60 ,,	+++	++	3	5	10		6	++				1	2	+++
10.69 ,,	+++	+												

Analyst: M. Väliranta

Table 2. *List of plant indicator species identified in the MIS 5a macro- and microfossil records from borehole 2/2010 with related mean July air temperature ranges determining the species' current northernmost distribution limit in Finland (in °C).*

Taxon	Median of July mean	July mean range
Callitriche cophocarpa	13.7	13.5-13.9
Potamogeton compressus	13.9	13.1-14.3
Ceratophyllum	13.9	12.9-14.1
Elatine triandra	15.2	14.5-15.9
Typha	15.7	15.1-16

Figure captions

Figure 1. A-C the Sokli Carbonatite Massif and direct surroundings with location of boreholes; **B** is a raw hill-shade map created from high-resolution (2 m) digital elevation data (Geological Survey of Finland CC BY 4.0 license; downloaded 2019/10). **D** borehole lithologies, chronology and types of proxy analyses. Local climate-stratigraphy is according to Helmens (2014). The MIS 5a deposit that is the topic of the present paper is highlighted with a yellow box.

Figure 2. A selected diatom and chironomid taxa, **B** other aquatic and wetland taxa, and **C** terrestrial plant taxa encountered in the fossil analyses of the MIS 5a deposit in borehole 2/2010. Shown in **A** are diatom taxa with values > 1 %, and selected taxa with values > 0.5 %, and chironomid taxa with $\geq$ 2 occurrence and $\geq$ 2 max abundance and N2 $\geq$ 2.

Figure 3. Pollen- (**A**), plant indicator species- (**B**) and chironomid-based (**C**) climate reconstructions for MIS 5a at Sokli. Fossil pollen assemblages are compared with modern pollen assemblages encountered in the calibration-set lakes in **A**1. The chironomid-inferred temperatures values are given with a locally weighted scatterplot smoother (LOWESS, span = 0.20; Cleveland, 1979) applied to the reconstructed values.